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Section B.—Biological Sciences.

The Geometry of Insect Pairing.

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In insects bilateral symmetry is practically universal, except in some minor matters, as, for example, the slight overlap of the elytra exhibited by many beetles. In the females the symmetrical condition may be taken to be almost universal, but the males in certain families exhibit asymmetry, which in some cases is very extreme, in the terminal segments of the abdomen. It is with this condition that the present paper deals, and the simplest course to pursue is, first to state the case as shown by some species of Diptera, that being the Order most familiar to the author and one in which an asymmetrical condition is comparatively common, then to outline a possible explanation of the phenomenon, in the course of which certain terms will be defined in order to clear the ground of existing ambiguities. Certain statements made in the course of the argument will then be justified as far as possible, and, finally, a few special points will be discussed.

In most insects, excluding such aberrant forms as the dragon-flies, the genital tube opens on the under side of the 9th abdominal segment, and the anal orifice is in the 10th. Let us trace a line in the vertical median plane of the insect, beginning on the dorsal side of the abdomen and proceeding round to the ventral side. On such a peregrination we shall first encounter the anal orifice and subsequently the genital one; this is true for all females and for most males, but there are some remarkable exceptions. Thus, it was shown by Snodgrass* that in the Asilid genera *Dascillis* and *Laphria* a different condition exists. On referring to the figures in that paper, it will be seen that on tracing such a line round the insect in its median plane the

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* 'Psyche,' vol. 9, p. 399.

genital orifice is met before the anal one; the hypopygium is then said to be "inverted." The term "hypopygium" will be used for the combination of the 9th and 10th segments, which are commonly fused into a single complex in flies, so that no movement of the one segment relative to the other is possible, and the two segments must always behave kinematically as a single body. This inversion is produced by the presence of a twist of 180° about the main axis of the body between the 6th segment and the hypopygium; the 8th segment is quite unsymmetrical and has an axial twist of about 150°; the hypopygium has the complete twist of 180°, but nevertheless it is practically symmetrical about the median plane which still bisects it. The result of this twist is to produce a true asymmetry, although it may not be very apparent on casual examination; in fact, not until the relative positions of the orifices are looked into.

This remarkable condition was long thought to be excessively rare, but Mr. F. W. Edwards has informed the author that it is found among the Nematocera in *Dixa*, in *Phlebotomus* (and probably in all Psychodidæ), in the Tipulid genera *Molophilus*, *Rhypholophus*, *Ormosia*, *Amphineurus*, and *Styringomyia*. In *Macromastix* the twist is usually incomplete. In Mosquitoes the condition is universal, and this case is of peculiar interest, as Christophers* pointed out that the twist occurs shortly after the emergence of the imago from the pupa. This is confirmed by Edwards in the case of *Styringomyia*; he informs me that he has dissected the pupa of specimens of that genus and finds the hypopygium to be normal in position, though it is inverted in the adult, as stated above. It is quite likely that further observation will largely extend the list of such cases.

As another example, long familiar to descriptive writers, that of the Syrphids may be cited; this is a more complicated form than that of *Dascillis*. One of the most highly differentiated forms of hypopygium is that of *Eristalis* and has been well figured by Berlese. The author has recently examined *Eristalis*, and the terminal segments, as seen in ventral view and in the passive state, are shown in fig. 1. All that is then visible of the hypopygial complex is the anal orifice with its two small side flaps; the rest is withdrawn into a sort of pocket, but the median plane is again very closely coincident with that of the insect. The link connecting it with the abdomen is, however, extremely asymmetrical; the base of the link is inserted far to one side of the median plane, and the tergites of the segments are turned round so that they are at right angles to the ventral plane; further, the 8th segment does not carry the hypopygium terminally, but grasps it sideways, like a hand holding a dumb-bell. In fig. 2 the hypopygium is shown just drawn out of the pocket, and, in addition to the anal orifice, one can now see two side flaps or claspers, *c*, *c*, and beyond these, when thus viewed

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* 'Indian Journal of Medical Research,' vol. 3, pp. 371–394 (1915).

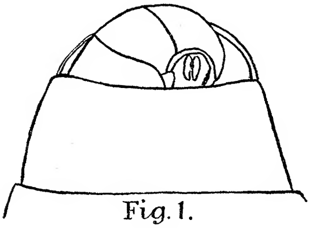


Fig. 1.

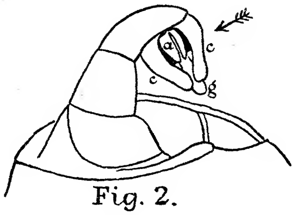


Fig. 2.

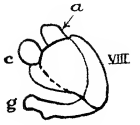


Fig. 3.

vertically, the male organ, *g*, or so-called penis. In general, Dr. Sharp's term, "œdeagus," will be used for this part of the complex. Fig. 3 gives a side view of the hypopygium as seen in the direction of the arrow of fig. 2.

As stated above, the median plane of the insect is practically coincident with that of the hypopygium, which is also practically symmetrical about that plane, but once more it will be seen that if we proceed from the dorsal side of the abdomen to the ventral, keeping in the geometric median plane, we meet the œdeagus before the anal orifice, so that there is a species of "inversion," though far more complex than the plain twist of *Dascillis.* The author has examined a few other Syrphids and finds that the arrangement is practically the same as that described above in *Helophilus* and *Rhingia,* and that it is kinematically equivalent in *Syrphus bistriatus,* though certain minor differences occur. Considerable hypopygial asymmetry occurs in many other families of flies, for example, in Dolichopodidæ, in Pipunculidæ, and in many Empids.

Before proceeding further, it is desirable to define certain terms that will be used to give precision to the discussion. It is unfortunate that many otherwise admirable descriptions of the phenomenon under consideration are rendered almost useless from a loose and inconsistent use of such terms as "bend," "twist," etc., the meaning of which in most cases can only be guessed at by the help of the context; it is therefore hoped that the terms suggested may prove useful.

The process of pairing consists essentially in the conjunction of two separate tubes, the male genital tube and the female genital tube, to form a single tube, which Dr. Sharp well designates the Genital Conduit. In order that the junction may be effected, the individuals concerned must be so placed that the one tube can be readily inserted into the other, and that the mechanical reactions called into play by that insertion can be taken up. The relative station taken up by the individuals *just previous to pairing* will be called the "Pose." The conditions appear to be consistent with but two possible poses: the simplest, and possibly the primitive one, is that in which the individuals are collinear, tail to tail, as shown in fig. 5; this will be called the "Linear Pose," and will be denoted by the letters L.P.; the necessary reaction to the pairing forces is provided for by the presence of a common platform. Mr. Edwards informed me that most Tipulids adopt this simple pose on pairing. The other pose is that in which the individuals are in a common vertical plane, the reactions being then transferred through the legs of the superior individual to the body of the inferior; this will be called the "Vertical Pose," and has two forms, according to which sex occupies the upper position; if that be the female it will be called the female vertical pose, and will be denoted by F.V.P., while the other case will be called the male vertical pose, and will be denoted by M.V.P.; the latter appears to be by far the commonest pose amongst insects.

The second important factor is the manner in which the tubes are related at the instant of pairing. Consider two individuals in L.P.; when the tubes are connected, the upper surfaces of each will be in contact, as will the lower; this condition (consequent on L.P.) will be called "Direct Correlation." Now consider a V.P.: the one tube can enter the other if a simple flexure be imposed on the terminal segments of either or of both individuals, but on conjunction in this pose it will be seen that the upper surface of one tube is against the lower side of the other; this will be referred to as "Inverse Correlation." One of the main questions to be dealt with is that of correlation, and, indeed, whether true inverse correlation ever occurs.

It is unfortunate that practically no records are available as regards either the pose or the correlation in the act of pairing; in many cases this is unavoidable; for example, with those insects that pair in flight. After pairing is accomplished, the insects commonly change their relative stations: the new configuration will be called a Position, and is usually the only

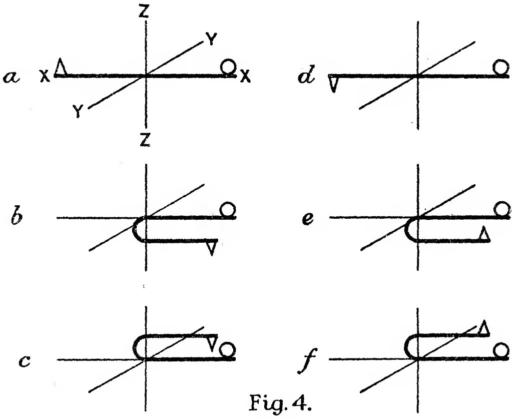
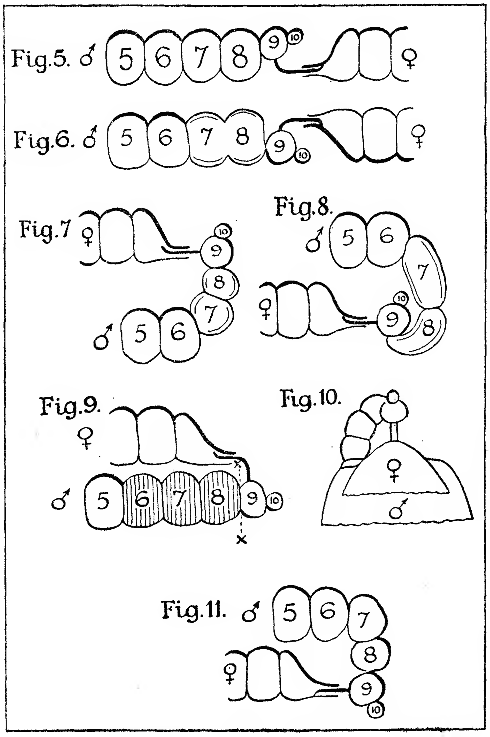


Fig. 4.

configuration that is recorded. The possible positions attainable from a linear one, directly following pairing in the linear pose with direct correlation, are shown in fig. 4, for which the author is indebted to Mr. A. Mallock, F.R.S. The axis XX is the original line of pairing, YY and ZZ the perpendicular axes, the former and YY lying in the plane of the pair. The female is taken as the reference individual, and a small circle is placed on the dorsal surface; the male's dorsum is similarly indicated by an arrow head. The possible resulting positions can be attained by rotations of 180° about the axes XX and YY; the former being round the axis itself will be designated a Twist, the latter being called a Flexure. It will be seen that four vertical positions can be derived from the original linear one, fig. 4, *a*. Of these, 4*b* involves ventral presentation, which occurs in *Bittacus* and a few other insects; 4*c* involves dorsal presentation, and is consequently "gripless"; the other two positions involve a preliminary Twist of 180°, as shown in 4*d*; they are respectively a female vertical position, 4*e*, and a male vertical position, 4*f*. But, if no relative rotation of the united genital tubes is possible after pairing, the hypopygium is, kinematically speaking, a part of the female; hence direct correlation in the last two cases involves an inverted hypopygium, owing to the 180° twist.

The conditions are better realised from figs. 5 to 8. Fig. 5 shows the initial condition, with direct correlation from a linear pose; fig. 6 gives the result of a twist of 180° thrown principally on the 7th and 8th segments, as is usually the case; fig. 7 shows the resulting F.V. condition, and fig. 8 the M.V. one. It will be noted that the latter involves the anal orifice being tucked up against the venter, a condition apparently not found in insects, in which what may be termed "a free anus," appears to be essential. The three conditions of direct correlation, vertical position, and free anus may be produced in the following manner. It is necessary to provide a twist of 180° about the axis of the insects and the flexure about the perpendicular axis: the latter may occur at any convenient place, say at the base of the œdeagus itself; indeed, in *Syrphus bistriatus*, evidence of a hinge can be detected there. The twist can be produced in two steps: segments 6 to 8 can twist 90°, presenting the tergites to the observer as in fig. 9, while the hypopygium can be given the remaining 90° twist relative to segment 8. This will result in the modified F.V. position of fig. 9. To attain the desired M.V. position, the female must, as it were, pass through the male. Let the insertion of the 5th segment be displaced laterally, that is towards the observer, let the remaining segments be flexed through some definite angle to form an arc, and let the hypopygium simultaneously rotate round the surface of the 8th segment through the same angle, about the line marked × in the figure. The resulting configuration, when the female has passed by the male, will be as shown in ventral view in fig. 10. This is exactly the condition figured for *Eristalis*. It is not suggested that the existing condition in that genus is the result of any such fantastic proceedings as the above, but it will follow that the actual form of asymmetrical male genitalia in that genus is explicable by the necessity of the three postulated conditions of free anus, direct correlation and male vertical position. It may be noticed that free anus and male vertical position are very simply attained, as shown in fig. 11, by a pure flexure, but that it then follows that the correlation is inverse. It would hence appear that the existing complexity is brought about by the necessity of preserving direct correlation.



If for any reason the necessity arose for pairing from a vertical pose accompanied by direct correlation, the twist of 180° must be present. This twist may either occur at the moment of copula, or be prepared beforehand, the latter is almost essential in flies that pair while in rapid motion or, still more so, in flight. It follows, then, that the condition under consideration can be explained by vertical pose having been adopted for some reason after direct correlation had become fixed in the species.

A condition similar to that of the Syrphids is found in the Dolichopodidæ, and is also well figured by Snodgrass in the 'Proceedings of the Californian Academy,' vol. 3, pp. 273–294. In that family the eighth abdominal segment is rotated till it lies on the side of the hypopygium, indeed it nearly hides it completely in some species, while the other side is completely free. The hypopygium is again practically symmetrical about the median plane of the insect, and the geometric relations are very like those of *Eristalis*, although the sideway displacement is here disguised by being concentrated at the junction of the hypopygium with the eighth segment; the foramen between the two is entirely lateral instead of terminal as in normal forms.

Although the evidence of the twist of the main axis is clear in the last two cases, it does not follow that this is always true. It is conceivable that a species which possessed direct correlation together with a M.V. pose, might lose all external evidence of the resulting twist in the process of evolution. In the absence of such external evidence it would then be impossible to distinguish the form thus modified from one in which simple flexure in the median plane, accompanied therefore by inverse correlation, was the condition that existed. In other words, one could not tell if it was a case of suppressed twist and direct correlation, or simple flexure and inverse correlation. The evidence may, however, persist internally, and it is of interest to note that Lowne points out that in *Calliphora* the sclerites of the 8th segment are seen on dissection to be quite asymmetrical, though external symmetry is otherwise exhibited. Further, Keuchenius states* that in the flies examined by him the testes were nearly always placed unsymmetrically, being sometimes twisted entirely to one side of the abdomen.

In the examples hitherto considered the 9th and 10th segments always moved as a whole, but in many insects it appears that the œdeagus is capable of independent motion. In such a case true somatic symmetry would exist to all external appearances, and any twist that might become necessary could be thrown entirely on the genital tube of the male, and consequently would only be discovered on dissection. If one peruses the classical paper by Sharp and Muir on the male tube in Coleoptera,† and studies carefully the descriptions and figures, many cases will be found in which extensive asymmetry occurs. For example, the Carabids have an œdeagus which twists round on its axis through some 90° on extrusion, and the same occurs in Dytiscids. Other forms of asymmetry appear to be not uncommon. It may be of interest to note that a clear account of pose and correlation in a beetle will be found in Mr. F. Balfour Browne's paper on *Hydrobius fascipes** where the rotation on copula observed in that Hydrophilid is described. Another good example of this form of asymmetry will be found in Harnisch's studies on *Lina populi*† in which he illustrates in detail the twisted œdeagus and the complex musculation involved in producing the twist.

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* 'Zeit. Wiss. Zool.,' Leipsic, 1913.

† 'Trans. Ent. Soc.,' 1912.

The explanation given above has involved two postulates which must be briefly dealt with; these are (1) the uniqueness of the initial genital lock and (2) a change of pose from L.P. to V.P. after direct correlation has been firmly established.

As regards the first, direct evidence can only be provided by the dissection of paired specimens, and such evidence is extremely scanty. In the papers of Sharp and Muir and of Harnisch, already referred to, there will be found figures showing the conditions existing in some Coleoptera. The co-adaptation is the well known one of a male eversible sac closely fitting the female vagina, in such a manner as to bring the end of the male duct into exact opposition to the spermathecal duct, and at the same time to obturate the oviduct. Such an arrangement must obviously become highly specialised and unique in its fit. The result is to form a completely closed tube from the testes to the spermatheca, and it may be suggested that a possible use of such a closed tube is that the necessary propulsive forces required for the injection of the sperm may be provided for by the mechanical action of the tube itself, such as by peristalsis, without drawing on the small store of energy in the spermatozoon. It may be pointed out that flies often have a pump of very perfect design placed in the lower part of the male duct which forces the sperm down that part; this is well figured by Nonidez in the 'Biological Bulletin,' 1921. But whatever be the reason, the existing evidence would appear to justify the statement that at some period a unique genital lock was developed. Even in those species in which the complete conduit is absent, and the sperm is simply deposited in the vagina, there is sometimes evidence of co-adaptation, as may for example be traced in Lowne's figures of the Blowfly genitalia. An interesting example of the persistence of such evidence in a species which has abandoned direct spermathecal storage is afforded by *Dytiscus*. Here the fertilisation is accomplished by means of a spermatophore, but the insect still has the twist in the œdeagus possessed by the land Carabids, showing that an early acquired character has been retained although the *raison d'être* has disappeared, and in spite of the condition being a possible source of embarrassment.

We must now deal with the second point, namely, the change of pose from linear to vertical. When pairing takes places with L.P., the reactions to the forces can only be taken up by the common platform; it follows that they must be submitted to willingly by both individuals. Hence, if the insects are capable of voluntary movements, the desire for pairing must be felt by both, and this probably involves that the germ cells in each are about equally mature. But a large number of species of flies exhibit protandry, probably due to the action of natural selection, and in such species the male cells are mature considerably before those of the female. It is then probable that the female psychology will involve a condition of non-acquiescence; but, whatever be the cause, it is quite usual to see the females repulse their partners; and, indeed, the whole complex of courting habits and sexual adornments implies a reluctant state of mind in the female. Therefore, in insects pairing in rapid motion, and inevitably in those which have acquired the more advanced habit of pairing in flight, a vertical pose is a necessity, which may be either the F.V.P. or the M.V.P. The former pose implies that the female is, as a rule, still the active partner in initiating the pairing, and this pose involves the simple inverted hypopygium. On the other hand, if the complete initiative is due to the male, it involves the M.V.P., with the consequent complications seen in *Eristalis*, etc.

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* 'Trans. Roy. Soc., Edinburgh,' vol. 47, p. 321 (1910).

† 'Zeit. Wiss. Zool.,' Leipsic, 1912.

Although it is true that the F.V.P. involves the female as being an active member of the pair, it does not necessarily follow that she is also willing. In cases where flight pairing has to be effected, certain Empids, as is well known, have developed a special solution of the problem. Thus, in *Empis borealis*, the male captures a prey which he presents to the female while both are in flight, and thus induces her to provide him with the necessary momentary grip required for pairing in the F.V.P. Mr. J. E. Collin, F.E.S., has observed the complete operation in that species, and has kindly informed the author of the details. The pose, and possibly the pairing, takes place with the male beneath on offering the prey: but the position of the insects, when pairing has been completely effected, is the more usual M.V. position. If the pairing is effected in the first, or F.V.P., this movement of necessity involves a 360° twist in the main axis; most Empids have highly complex male appendages, but the working out of the case, in detail, must await further information as to the conditions of pose and correlation.

It is convenient at this point to refer to the case of mosquitos which always have an inverted hypopygium. The observed final position of pairing is said to be either the simple linear one, or its kinematic equivalent, the position of venter-to-venter, either of which, if combined with direct correlation, involves the undoing of the initial twist. The pairing of *Stegomyia fasciata* has been described by Banks.* He states that he has repeatedly instantaneously killed pairs in copula and they are invariably in the venter-to-venter position, the male clasping the female with his two front pairs of legs. He further states that the method of pairing is for the male to fly under the flying female, and then clasp her in the same way. If the statement be taken literally, it would appear to involve the male flying upside down at the instant of pairing, which may indeed be just possible, but offers considerable mechanical difficulties. It is possible that, at the first instant of copula, the condition is the same as in *Empis borealis*, namely, an ordinary F.V.P., as is indicated by the inverted hypopygium, and that the change to the observed final position is made with extreme rapidity, as indeed appears to be the case with that species; the reversal of twist involved in the change can readily take place in soft-bodied insects such as the Culicids. A suggestion may be offered as to the method by which the female is induced to give the necessary initiation to the grip. In the Empid genus *Hilara*, the initial grip is induced by the male presenting to the female a bogus prey made up of a fine-spun silk balloon; it is possible that the enormous palpi, so characteristic of many Culicid males, may play a similar part in their case.

Hilara affords a possible example of another method of providing for the twist necessitated by a change of position after pairing. It has been seen that *Empis borealis* in the act of pairing executes a change from the F.V. position to the M.V. one, and if the copula has been effected in the former position, this involves a twist of somewhere about 360° in the main axis. *Hilara* has similar courting habits, and may possibly execute the same evolutions. Now it is remarkable that the insects of this genus possess a very peculiar œdeagus, which takes the form of a long thread which is curved and even doubly curved in its length; the tubular thread is very highly chitinized, and, in consequence, is capable of but little torsion. It may be worth pointing out that the curving of the tube endows it with power of sustaining torsion. This "geometric torsion" was pointed out to the author by Dr. G. T. Bennett, F.R.S., and is attained as follows:—Let two parallel axes be connected by a flexible but non-torsionable tube, fig. 12. If the

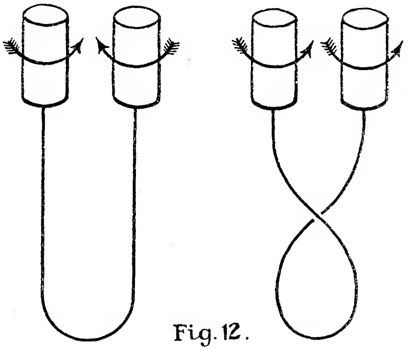

Fig. 12.

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* 'Philippine Journal of Science,' vol. 3A, p. 296 (1908).

ends of the tube be turned in opposite directions, it will merely roll round on itself; but if they be turned in the same direction, the two halves will wind up into a sort of double rope. Such a state of affairs being granted, it is then possible to hold one of the ends fixed, while the other end can execute a certain amount of rotation in spite of the fact that the tube itself is non-torsionable. It is possible that this property is utilised in the pairing of *Hilara* and allied forms.

Although many families of flies exhibit the asymmetry we have been dealing with, there is no doubt that male vertical pose is adopted by most of the higher forms, and that to all appearances the males are symmetrical; any evidence of the twist, consequent on the adoption of vertical pose with direct correlation, may thus have disappeared. A good account of the mating of such flies will be found in Sturtevant's paper on the North American Species of Drosophila,* while practically the only complete account of the details of fertilisation will be found in Nonidez's paper referred to above, dealing with the process in *Drosophila melanogaster*. The sperm is merely deposited in the vagina and the spermatozoa make their own way into the spermatheca, the ovarian obturation being produced by the presence of an egg in the duct. The necessity of a closed genital conduit has apparently been supplanted by the adoption of some chemotactic process; in such cases it is probably impossible to determine the correlation, and, indeed, the necessity for it having vanished, there may be no true correlation present.

Nevertheless, the author trusts that he has made out a case for the thesis that the primitive pose of insects was probably the linear one, and that the elaborate forms of hypopygium found in so many flies are due to the secondary assumption of a vertical pose combined with the persistence of the direct correlation imposed by the original primitive linear pose.

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* 'Carnegie Institute Publications,' p. 301 (1921).